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Effect of Competition on Survival in Western Oregon of the Douglas-Fir Beetle

Dendroctonus pseudotsugae Hopkins (Coleoptera: Scolytidae)

By
Richard F. Schmitz
Julius A. Rudinsky

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Forest Research Laboratory
School of Forestry
OREGON STATE UNIVERSITY
Corvallis

AUTHORS

RICHARD F. SCHMITZ was formerly a research assistant in the Department of Entomology, Oregon State University. At present he is research entomologist with the Forestry Sciences Laboratory, Intermountain Forest and Range Experiment Station, U.S. Forest Service, at Missoula, Montana.

JULIUS A. RUDINSKY is Professor of Forest Entomology, Department of Entomology, Oregon State University.

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SUMMARY AND CONCLUSIONS

The studies described were designed to measure the effect of intra- and interspecific competition on the Douglas-fir beetle in the field and laboratory. The studies revealed that the intensity of competition can be regulated by several factors. Attacks of the Douglas-fir beetle ceased either when air temperatures dropped below 50 F, or when it rained. Cool rainy periods are characteristic of April and May in western Oregon, so the frequency and duration of attack are regulated in part by weather. Attack density and brood survival along the boles of the study trees were such that intraspecific competition was most likely to occur on the underside of the top one-half of a down tree.

Most eggs were laid within the first 5 inches of egg gallery. Equal numbers of eggs were laid alternately on the left and the right sides of the egg gallery. This alternate arrangement increased the possibility of survival when overcrowding took place. We did not note a difference in the number of eggs laid at attack densities ranging from 1 to 3 to a square foot, but average gallery lengths were 4.5, 10.2, and 8.7 inches at attack densities of 1.2, 2.8, and 3.2 for each square foot.

Maximum survival of broods was recorded in the laboratory when one attack occurred for each 1.5 square feet of phloem, and when 1.6 to 2.0 square inches of phloem were available for each larva. Under cages in the field, maximum survival of broods occurred at attack densities from 1.0 to 1.9 to a square foot, from 50 to 100 larval mines for each square foot, and from 2 to 19 inches of egg gallery for each square foot. Survival decreased with increases in attack density, total length of egg gallery, and number of larval mines for each square foot. We also recorded maximum survival of broods in the field when each larva had from 2.6 to 3.0 square inches of phoem in which to develop. With from 3 to 6 attacks to the square foot, the increase ratio was about 1:1.

Interspecific competition was not a factor in natural control of the Douglas-fir beetle in the studies described.

In general, our study revealed intraspecific competition to be an important natural control of the Douglas-fir beetle, and its effect must be considered in any prediction of population trend. This type of study, however, measures the effect of intraspecific competition on the brood from only the initial attack. Because some re-emerging parents undoubtedly produce additional broods, the net effect of intraspecific competition on population trend cannot be determined until these broods are considered. Similarly, an accurate measure of the effect of entomophagous insects in reducing brood densities is also needed. Finally, the nutritional requirements of the beetle and the implications of phloem quality on beetle survival need to be studied before a refined assessment of the effect of intraspecific competition can be made.

EFFECT OF COMPETITION ON SURVIVAL IN WESTERN OREGON OF THE DOUGLAS-FIR BEETLE

Dendroctonus pseudotsugae Hopk., (Coleoptera: Scotytidae)

By

Richard F. Schmitz and Julius A. Rudinsky

INTRODUCTION

The overall objective of this investigation was to determine the effects of inter- and intraspecific competition on survival of the Douglas-fir beetle in western Oregon in windthrown or down trees. The specific objectives of this study were: to determine how the beetle's biology and behavior influence the intensity of competition, to determine the phloem area necessary for normal development of an individual Douglas-fir beetle larva, to assess the effects of intraspecific competition, and to measure the effects of interspecific competition on survival of the Douglas-fir beetle.

The Douglas-fir beetle, Dendroctonus pseudotsugae Hopkins, is the most destructive insect pest of Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, one of the most important timber species of western North America. The beetle is native to North America and kills saw-timber throughout the range of the host tree.

In coastal forests, the beetle normally infests windfalls, logging slash, and trees weakened by fire or drought. When a beetle population increases sufficiently to exhaust its supply of this susceptible material, it invades and kills standing green timber.

The most destructive outbreak in this region occurred from 1949 to 1953 after wind toppled 10 billion board feet of timber in western Oregon and Washington. Johnson reviewed the factors associated with Douglas-fir beetle outbreaks, and noted that Wright (Johnson 1960, 11-12) believed droughty conditions probably prolonged the outbreak by making standing timber susceptible to attack. The resulting outbreak of beetles killed three billion board feet of standing timber. A similar outbreak followed the typhoon of October 12, 1962.

Such outbreaks emphasize the need for accurate methods of forecasting the trend of Douglas-fir beetle infestations so that measures can be initiated to prevent large-scale tree killing. Such forecasts require an understanding of the environmental factors that limit population increase and knowledge of the insect's ability to increase under optimum conditions.

Competition for food and space is one of the more important factors that limits the rate of multiplication and survival of an insect. Milne (1961) defines competition as "The endeavor of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing, when that supply is not sufficient for both (or all)." Competition may occur within a species (intraspecific) or between several species (interspecific).

McCowan and Rudinsky (1958) observed that when the density of successful Douglas-fir beetle attacks was more than eight to a square foot of inner bark, many larvae died. McMullen and Atkins (1961) noted that the increase in progeny declined from 22:1 at densities of one attack a square foot to 1:1 at attack densities of 13-17 a square foot. Similar relations have been found by other investigators studying the effect of competition on the survival of other scolytids (Cole, 1962; Kangas, 1953; Knight, 1961; Miller and Keen, 1960; Nuorteva, 1954; Reid, 1963; Thalenhorst, 1958).

The effect of interspecific competition on the survival of the Douglas-fir beetle has received little attention. Several investigators (Bedard, 1938; Johnson, 1960; Walters and McMullen, 1956) have compiled lists of insects commonly associated with the beetle, but they have not attempted to measure the effect of the competition resulting from these associations.

METHODS OF STUDY

We conducted the study in the field and in the laboratory during 1960 and 1961. Field investigations were performed 14 miles west of Corvallis, Oregon, on the Marys Peak Watershed, Siuslaw National Forest. The watershed contains Douglas-fir with some western hemlock, Tsuga heterophylla (Raf.), western redcedar, Thuja plicata Donn, and grand fir, Abies grandis (Douglas). Trees used in the field studies either were windthrown or were felled by sawing.

Study Areas

Field investigations were conducted in four areas on the Marys Peak Watershed. Time and duration of attack and pattern of infestation were studied at two localities. In one area at 2,000 feet elevation (study area A) six mature trees, about 175 years old, were selected for study after they had been windthrown in November 1959. In the second area at 1,450 feet elevation (study area B) eight young-growth trees, 75 years old, were felled between November 1959 and April 1960. Exposure of the mature windthrown trees ranged from full sunlight for portions of the day to almost complete shade. The young-growth trees were in partial shade most of the day. Daily records of temperature and humidity were obtained from hygrothermographs maintained at the two study sites. Daily records of rainfall and cloud cover were obtained from measurements taken by Oregon State University at Corvallis.

We also studied, in two areas, the effects of competition on beetle survival under field conditions. In one area at elevation of 1,980 feet (area C), the trees averaged 214 years old, and at a second area at elevation of 2,000 feet (area D), the average tree was 207 years old. The study tree felled in each area was in shade most of the day. Areas C and D were Site III or Low Site III.

Rate of oviposition and effects of intraspecific competition were studied in the laboratory. In both field and laboratory experiments any exposed wood, such as cut ends of logs, was coated with paraffin to retard drying that might have affected activities of the beetles.

Attack Pattern and Oviposition

During 1960, we investigated attacks to measure their temporal and spacial distribution. The temporal distribution was studied to

determine if late-season attacks encountered interference from previously established broods. Spacial distribution of attacks was recorded to measure the density of beetle attacks and of entomophagous (insect-eating) insects along the tree bole. We conducted laboratory studies to determine if density of invasion influenced the pattern of oviposition.

Each new attack, on six study trees at site A and eight trees at site B, was marked with colored staples. A different color or combination of colors was chosen at each inspection (about a week apart) to differentiate the date of attack. All attacks were marked on the young-growth trees, but only those on the base, midbole, and crown of the old-growth trees were marked because of the large size of these trees. In old-growth trees the basal sample was located 30 feet from the root collar. The midbole sample was about halfway between the basal sample and the center of the live crown. The uppermost sample was located about midway into the live crown at a point below the upper limit of infestation. These samples extended around the circumference and 5 feet along the bole.

The effect of the infestation pattern of the Douglas-fir beetle on brood survival was assessed by removing bark samples from all study trees at three bole positions: butt, midbole, and top. The number of successful[1] and unsuccessful Douglas-fir beetle attacks, number and length of egg galleries, number of larval mines, and the number of live brood were recorded for each of these samples. Cocoons of Coeloides Wesmael (Braconidae), larvae of Enoclerus Gahan (Cleridae) and larvae of the genera Medetera Fisher Von Waldheim (Dolichopodidae) and Lonchea Fallén (Loncheaidae) were counted because of the potential importance of these wasps, checkered beetles, and flies as parasites and predators on the Douglas-fir beetle.

Three sections, each 3 feet long, were cut from the midbole of each of two green uninfested trees and brought to the laboratory for studies of oviposition. The sections were individually caged in a greenhouse, and beetles were introduced to obtain about 8, 2, and 1 or fewer attacks for each square foot. We attained an approximately even distribution of attacks over the bark surface of these logs by introducing the beetles into the cages at noon, when all bark surfaces were evenly illuminated.

Beetles were collected for this study from bole sections of a tree infested under field conditions, and were sexed by means of the

[1]A successful attack is an attack that has at least one larval mine originating from the egg gallery constructed by the female beetle. An unsuccessful attack is an attack that lacks any larval mines.

roughened elytral declivity of the female and the stridulation produced by the male (Hopkins, 1909, Jantz and Johnsey, 1964). Males and females collected each were divided equally among the six caged sections.

Eggs laid on each gallery and the number in each successive inch of gallery were recorded on each of the six logs. Measurements were made by excising a strip of bark, about 1 inch wide, enclosing that portion of the egg gallery that the female beetle had recently constructed. A portion of the gallery was left intact to avoid disturbing the female, and the exposed wood was paraffined to retard loss of moisture. When the beetles began constructing gallery, the number of eggs in each inch of gallery and the side of the gallery on which they were deposited were observed with the aid of a dissecting microscope.

Phloem Tissue Utilized During Brood Development

Because studies of phloem utilization were conducted in the laboratory, the brood of an individual female could be reared free from interference by other broods. This method of studying competition eliminates, in large part, the mutual interference that results when the area of phloem tissue is kept constant and the number of insects is increased. Klomp (1964) discussed the difficulty of separating the effects of mutual interference from those of competition, where the method of study includes increasing the insect numbers and holding the amount of food constant.

Preparing the study sections

We determined the area of phloem tissue needed by a brood to develop from egg to adult by infesting predetermined areas of phloem with one pair of adult beetles. The areas were delineated on 3-foot-long sections of Douglas-fir bole with templates of three shapes and three sizes. After boundaries were marked on the bole, a strip of bark, 1 inch wide, was removed around the perimeter of the area, down to the wood. This strip served as a barrier to keep the egg-laying female and the developing larvae within the desired area (Figure 1).

Logs containing the beetles used to infest the bole sections were collected in the field and stored in a room at 38 F. When we needed beetles, the logs were placed in a room at about 75 F, and emerging beetles were collected. A female beetle was inserted into a hole of 1/8-inch diameter drilled through the outer bark at the base of each log section. We secured a gelatin capsule or a piece of wire screen over the hole to confine the beetle. After one day, a male was placed in the entry hole. Surviving brood were counted after the callow adult stage had been attained after about 50 days.

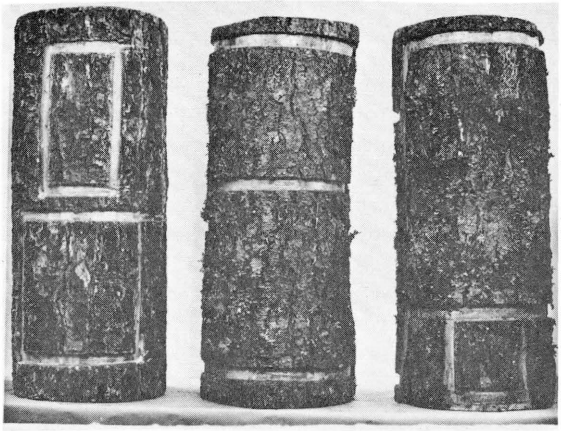
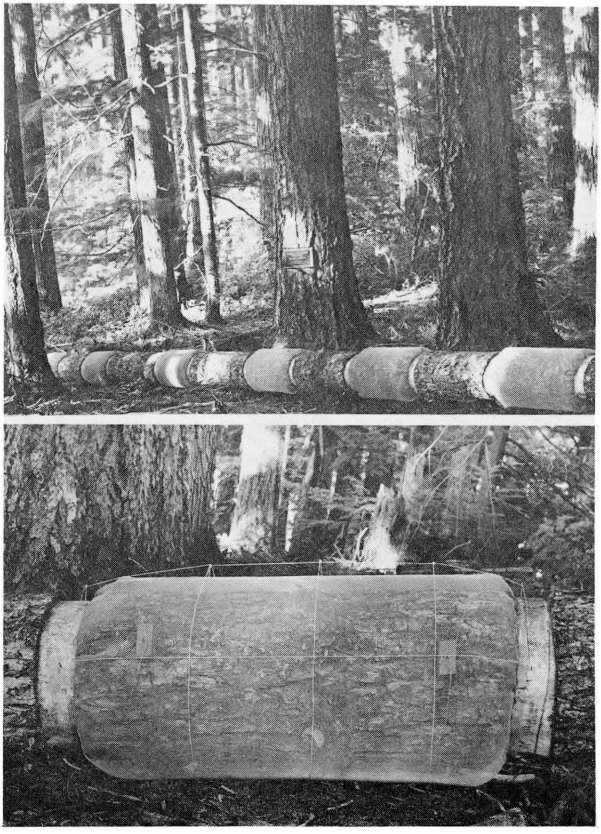


Figure 1. Bole sections used to study survival of Douglas-fir beetle brood in six areas ranging in size from 6 by 6 inches to 18 by 24 inches.

Figure 2. Tree at study area C showing the alternate arrangement of the 4-foot-long caged and uncaged bole sections (above). Cage on the tree at area C showing construction detail (below).



We conducted three such studies in the laboratory from September 1960 to April 1961. The first trial involved six sections, 3 feet long, cut from the midbole of a 70-year-old Douglas-fir. The bark of these bole sections was delineated into areas 6 inches wide and 12 inches long, or 12 inches wide and 12 inches long. Two areas of each dimension were marked on each bole. To minimize possible difference in the phloem between areas on a single bole, we placed a small and a large area one above the other, their relative positions being reversed on opposite sides of the bole. The 12-inch dimension was parallel with the long axis of the bole section. Placement of the four developmental areas on each of the six sections provided 24 areas for study.

During the second trial, 12 sections, 3 feet long, were cut from the midbole of a 160-year-old Douglas-fir. Six differently sized areas of phloem were delineated on the bole sections. The six areas were $\frac{1}{4}$ square foot (6 by 6 inches), $\frac{1}{2}$ square foot (6 inches wide, 12 inches long), 1 square foot (12 by 12 inches), $1\frac{1}{2}$ square feet (12 inches long, 18 inches wide), 2 square feet (16 inches wide, 18 inches long), and 3 square feet (18 inches wide, 24 inches long). Two of the six differently sized areas were placed on each side of a bole. We grouped together the $\frac{1}{2}$- and 1-square-foot areas, the $\frac{1}{4}$- and 3-square-foot areas, and the $1\frac{1}{2}$- and 2-square-foot areas (Figure 1). This arrangement provided eight replications of each size for study. The areas were aligned so that the long dimension was placed parallel to the long axis of the bole.

The third trial included 12 bole sections; six were cut from each of two Douglas-fir trees, 74 and 82 years old. The study areas had the same arrangement, alignment, and dimensions as those in the second trial. To minimize any difference in phloem tissue between trees, we placed two of the four study areas of any one size on two bole sections from each host tree.

Measuring brood survival and phloem utilized

Surviving brood and first instar larval mines were counted after about 50 days. We calculated survival by dividing the number of live brood by the number of first instar larval mines. The area of phloem utilized by each brood was measured to the nearest 1/10 square inch with a dot grid scribed on clear cellulose acetate.

A strip about $\frac{1}{4}$ inch wide was added to the perimeter of phloem mined by the brood because we observed that the phloem deteriorated for about $\frac{1}{2}$ inch beyond the terminus of the larval mines. Where two broods occupied a limited area, the larvae would avoid this strip of deteriorated phloem; it was included, therefore, in the measured area of phloem.

Beetle attacks, larval mines or larvae, and inches of egg gallery for each square foot are common indices of population density. Among these, the number of larvae or larval mines best describes intensity of competition. In this study, we designed an index to express competition experienced by a single larva.

We computed the index, called the "phloem factor," by dividing the area of phloem mined by a brood, plus the $\frac{1}{2}$-inch buffer strip, by the number of larval mines. This index represents the average area of phloem available to each first instar larva.

Field Studies of Effect of Intraspecific Competition

Windfall was abundant during the winter of 1960-1961, and the attacks in 1961 were not expected to exceed 1 or 2 to a square foot. Therefore, we studied the effect of intraspecific competition on brood survival under caged conditions to attain higher densities of attack.

Caging and infesting trees

To provide a range of attack densities, six cages, 4 feet long, (Figure 2) were placed on the midbole of the down trees at study areas C and D . The mid-portion of the bole was caged because studies by Furniss (1962), and McCowan and Rudinsky (1958) and our results obtained during 1960 showed that survival of brood and number of beetle attacks were least variable at midbole. Caged and uncaged areas were alternated along the midbole to study intraspecific competition with and without the influence of entomophagous insects. A strip of bark, 4 inches wide, was removed from between the adjacent areas to prevent the movement of insects under the bark from caged to uncaged areas. Wire hoops fastened to wooden blocks held the screen off the outer bark. To determine the distribution of beetle attacks within the cage, the screen was divided with string into areas containing 1 square foot, or less (Figure 2).

To supplement the 12 caged sections on the two study trees, 48 sections, 3 feet long, were cut from the midbole of four live dominant Douglas-fir trees, two from each area. Twelve of the 24 sections cut at each area were caged to facilitate regulating the density of Douglas-fir beetle attack. The remaining 12 sections were left uncovered, and thereby, subject to infestation by predators, parasites, and associated insects.

Controlling attack density

Based on the previous laboratory studies that provided an incication of the area of phloem needed for maximum survival of an individual brood, an attempt was made to infest the bole sections to three densities. To eliminate overcrowding, a low density to average less than 1 attack for each square foot was established. The medium intensity of attack was set at 1 to 3 attacks for each square foot. At this density some intraspecific competition was anticipated. So that we could study intense intraspecific competition, a density of 8 or more attacks for each square foot of bark was desirable.

The 4-foot-long caged areas on each down tree were numbered consecutively from 1 to 12, beginning with the area nearest the base of the tree and continuing toward the crown. The six odd-numbered areas were caged, but the six even-numbered areas were left uncaged. The caged areas were infested to the following densities: areas 1 and 7, low density; areas 3 and 9, medium density; and areas 5 and 11, high density. Similarly, attempts were made to infest uncaged areas as follows: areas 2 and 8, low density; areas 4 and 10, medium density; and areas 6 and 12, high density. This arrangement was designed to reduce variation in survival, which might result from differences in the phloem between the caged sections. Caged sections were infested over a one-week period. Beetles were sexed, divided equally among the cages to be infested during any one day, and released within 24 hours of collection.

We recorded distribution of attacks around the bole after each introduction of beetles by using the square-foot grid marked off on each cage (Figure 2). In this manner, if only the underside of the bole was being densely infested, beetles were no longer introduced into the cage. To help achieve a density of 8 attacks for each square foot of bark, more females than males were introduced at any one time to keep the bole attractive to beetles introduced later.

Sampling brood survival

Bark samples on the down trees were removed in November 1961, after the brood had reached the callow adult stage and development had ceased for the season. Bark within the caged portions of the down trees was carefully removed in three pieces. The shaded and sunlit parts of the top half of the 4-foot-long sections were divided into two equal parts. The lower half was removed intact. The bark was taken to the laboratory for final measurements and counts. Sections were kept at 40 F until we examined them. The area of phloem mined by the brood, length of egg galleries, number of larval mines, survival rate, and phloem factor were determined. Callow adults were counted by excavating them from the phloem with a knife.

The area of phloem mined by larvae that survived to the callow adult stage was measured for five larval mines from each of the 12 study sections. We did not measure larval mines that callow adults had extended by further feeding. The area of larval mining was traced on paper and measured to the nearest 1/10 inch. We also recorded lengths and depths of each of these larval mines, and measured the thickness of adjacent phloem.

Field Studies of Interspecific Competition

The temporal and spacial distribution of insects providing interspecific competition was recorded concurrently with the data tallied on Douglas-fir beetle attack at study areas A and B. The bark samples taken to study interspecific competition were the same as those to measure the temporal and spacial distribution of Douglas-fir beetle attacks. On young-growth trees, a fourth sample was removed just above the upper limit of Douglas-fir beetle attack to determine if Douglas-fir beetle galleries were intermingled with those of other scolytids normally infesting the upper boles of young trees. The number of attacks of competing scolytids and the incidence of mining by buprestids was recorded from each sample.

RESULTS AND DISCUSSION

Attack Pattern and Oviposition

Seasonal attack period

Douglas-fir beetle attacks were first noted on the experimental trees at study area B on April 9 and at area A on April 22. Attacks recorded on any one date ranged between 1 and 24 percent of the season's total; new attacks were marked on 10 of 12 weekly examinations at study area A and 10 of 14 weeks at area B. The last attacks were marked on July 11, 82 days after initial attack.

Weekly counts of beetle attacks revealed that peak periods of attack coincided or followed periods of sunny weather when air temperatures ranged from about 60 to 65 F. Periods of attack were broken by rain and temperatures below 50 F. Warm sunny periods, interrupted by cool rainy weather characteristic of April and May in western Oregon, and variation in exposure of over-wintering beetle populations combine to limit the duration of flight and attack periods. Such regulation of the attack period undoubtedly has an influence on final densities of attack. For example, additional susceptible host material might be created between periods of attack, perhaps resulting in a portion of the beetle population being attracted to the fresh material rather than to that already attacked. Atkins and McMullen (1962) suggested that under optimal conditions for flight, beetles may fly greater distances, which would tend to dilute the population and result in lower densities of attack.

We recorded the seasonal attack pattern on the bottom, middle, and top sample areas for four selected trees at study area B (Figure 3). In almost all instances, beetle attacks were recorded each week on the bottom, middle, and top position sampled on each tree. The beetles did not show a distinct preference for any particular portion of these trees during the attack period. Similar attack patterns were noted on the other study trees at both areas. At the recorded attack densities, there was no indication that initial attack and subsequent mating and brood development made the host material unattractive to beetles attacking later in the season.

The attack periods were about equal in duration at both study areas, but a higher total number of attacks was recorded at area B. The average number of attacks for each square foot of bark surface was 1.1 at area B and 0.5 at area A. Examination throughout the attack period revealed a gradual reduction in length of egg galleries and number of first instar larval mines to a gallery.

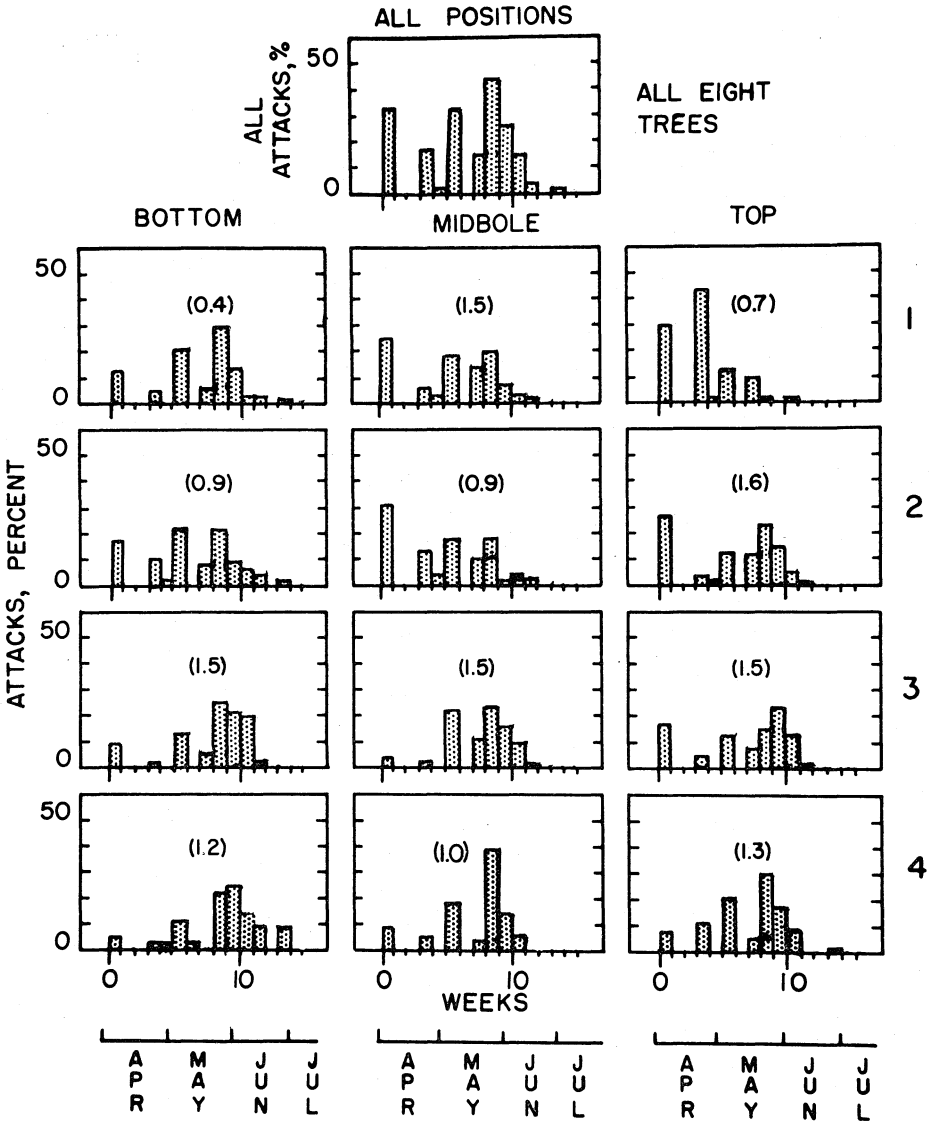


Figure 3. Weekly percentages of all attacks of the Douglas-fir beetle from 14 weeks during 1960 on eight trees at study area B (Top). Attacks are shown for bottom, midbole, and top sections of four trees at study area B (numbered at right). Attack densities to the square foot are shown in parentheses.

We compared the number of successful attacks, average length of egg gallery, and average number of first instar mines to a gallery established during 10 weekly periods in 1960 (Figure 4). The range in attack density on the eight trees at area B was from 0.8 to 1.7 for each square foot and from 0.3 to 1.1 on the six trees at area A. Attack densities were well below the level at which intraspecific competition was noted in the present study, and less than the 4 to 8 for each square foot McMullen and Atkins (1961) determined to be optimum for brood survival in the intermountain region of Canada. It is unlikely, therefore, that much of the reduction in egg gallery length and number of first instar mines can be attributed to competition for space. Possibly this reduction is the result of drying of the phloem.

Spacial attack pattern

We summarized the data recorded from the 14 experimental trees at study areas A and B (Table 1). The crown portion of trees 2,

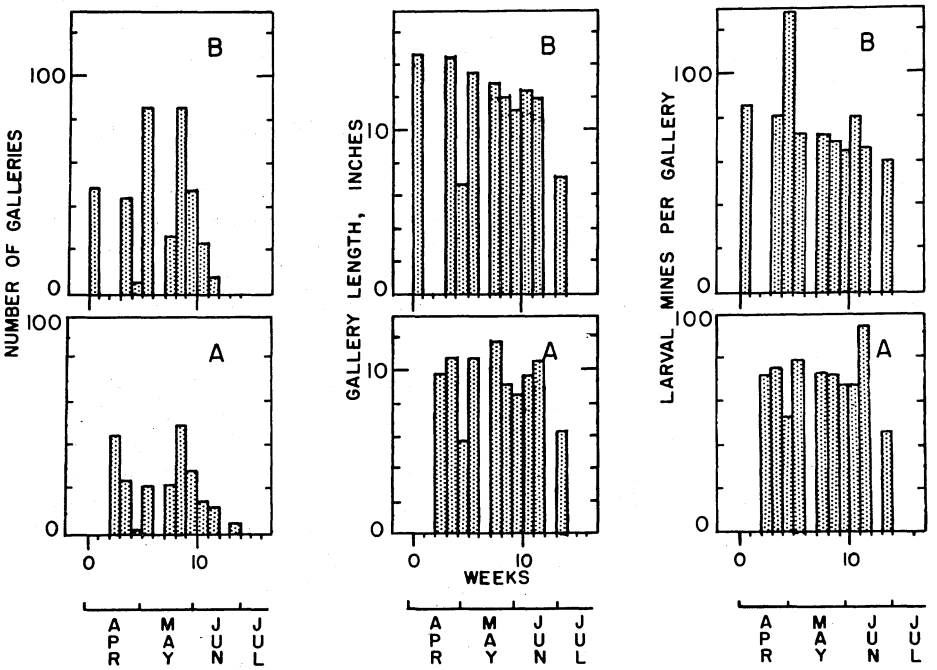


Figure 4. Number and average length of successful egg galleries and average number of first instar mines to a gallery for galleries initiated during ten periods of the 1960 attack season on eight trees at area B and six trees at area A.

5, and 6 at study area A was separated from the remainder of the tree bole when windthrown, and a "sour sap" condition developed that resulted in the outer bark becoming tightly adhered to the wood. This condition prevented removal of the topmost bark samples on these trees; therefore, no data were recorded from these samples.

Larval mines were more abundant and length of egg galleries in a square foot of bark was greater in the top half than in the lower half of the bole in the old-growth trees at study area A and the younger trees at area B (Table 1). However, the surviving brood in the younger, thinly barked trees at area B were most numerous at the base and declined in abundance toward the crown of the tree, possibly because the top of the tree dried more rapidly than did lower sections. In total, entomophagous insects were most numerous at the midsample, less numerous on the top sample, and fewest on the bottom sample (Table 2).

Based on these results and those of McCowan and Rudinsky (1958) and Furniss (1962), it appears that intraspecific competition of the Douglas-fir beetle will probably be more intense in the top half of the bole than in the lower half. At the same time, the density of entomophagous insects in this region might reduce the intensity of competition by feeding on some of the competing larvae.

The number of beetle attacks on the top and underside of logs was compared on 15 sample sections from the trees at area B. The underside averaged 1.3 attacks to the square foot, but the top surface averaged 1.2. Average survival on the underside was 28 percent, and 19 percent on the top surface. Egg galleries in the bottom half of the 15 samples totalled 320 inches more than in the upper surface. Of the predators, only the Diptera were more abundant (1 to the square foot) on the undersurface than on top.

Attacks in late season are made more frequently on the underside of down trees than on the upper surface. Attacks on the top half of the 15 samples during April, May, and June averaged 30, 31, and 39 percent of the total for the season. In contrast, attacks recorded on the underside during the same months averaged 20, 23, and 57 percent of the total. These data indicate that in the thinly barked upper portion of the bole, intraspecific competition would probably occur more frequently on the underside than on the top of the down tree.

Number and arrangement of eggs

Attempts to infest six bole sections to desired attack densities in the laboratory were only partially successful. The two densities of no more than 1 attack, or of about 2 attacks, to the square foot were readily attained (Table 3). But three attempts to infest two of the study sections to densities of 8 attacks to the square foot failed. When about

Table 1. Invasion Density and Brood Survival of the Douglas-fir Beetle on the Bottom, Middle, and Top Sampling Positions of the 14 Trees Examined during 1960 at Areas A and B, and Averages for Each Area.

Sample size			Egg galleries			Larval mines			Survival			Parent gallery[1]		
Bot	Mid	Top	Bot	Mid	Top	Bot	Mid	Top	Bot	Mid	Top	Bot	Mid	Top
Sq ft			Per sq ft			Per sq ft			Percent			In. per sq ft		
East Trail (area A)														
39.0	30.0	21.5	0.0	0.8	--	2	59	--	0	34	--[2]	0.4	7.9	--
42.0	32.0	30.0	0.0	0.8	1.4	0	65	109	0	40	13	0.0	8.1	14.7
41.5	34.0	27.0	0.1	1.8	--	5	69	--	12	15	--[2]	0.8	10.6	--
37.5	30.5	23.5	0.5	1.0	--	43	71	--	16	44	--[2]	5.1	11.0	--
55.0	44.0	34.5	0.0	1.1	--	0	65	--	0	21	0	0.0	9.1	--
42.5	31.0	25.0	0.3	1.5	1.7	28	118	110	39	45	26	3.2	15.3	16.3
42.9	33.8	26.9	0.1	1.1	0.5	19	75	109	22	33	19	2.7	10.3	15.5
Woods Creek (area B)														
20.0	22.5	19.5	1.5	1.5	0.7	99	73	50	54	47	15	23.8	19.1	9.2
26.5	18.0	22.0	0.9	0.9	1.6	60	71	105	39	23	20	9.6	16.9	19.7
20.0	17.5	15.5	1.5	1.5	2.4	97	94	110	27	19	21	17.7	18.4	18.2
21.5	18.0	16.5	1.2	1.0	1.3	101	98	95	29	12	10	12.1	15.0	14.0
20.0	15.5	12.5	0.9	1.3	1.0	48	83	70	51	43	11	7.0	16.0	9.6
22.0	19.5	17.5	1.1	1.3	0.5	83	86	35	31	18	36	10.9	15.9	6.6
21.0	17.5	16.5	0.8	0.8	0.6	96	76	54	30	16	33	15.0	14.0	7.6
21.0	18.0	17.5	1.3	2.6	2.0	98	172	153	47	13	18	17.6	32.2	23.1
21.5	18.3	17.2	1.3	1.6	1.4	85	94	84	42	22	19	14.2	18.4	14.7

[1] Successful galleries only.

[2] Sour sap.

2 attacks to the square foot of bark surface had been made on the caged bole sections, the introduction of additional beetles failed to increase the attack density. The additional beetles crawled about the cage and on the log, but failed to establish attacks. Dissections of these added beetles revealed that errors had not been made in sexing; both males and females were included in the group of beetles that failed to enter the study sections. The data indicated that the number of beetles released into the cages exceeded the number of beetles necessary to attain the final attack densities (Table 3).

Rudinsky (1963) has shown that the attractiveness caused by virgin female beetles feeding in fresh phloem tissue is considerably reduced by mating, so the method followed to infest the boles may have been responsible for the failure to obtain high densities of invasion. Male and female beetles were introduced simultaneously each day for a week. Possibly the immediate presence of the males may have suppressed the attractiveness of the female and discouraged further attacks. The normal olfactory behavior of the beetle may have been further influenced by the presence of the six study sections in the same room, from which odors of various degrees of attractiveness may have been emanating.

In all, 67 galleries were examined from three of the study sections (Table 4). Generally, the long galleries contained more eggs to the inch than the short galleries. The weighted average number of eggs laid in each inch of gallery for all categories was 7.7. This figure compares with an average of about eight eggs for each inch of gallery as reported by Furniss (1962) in studies conducted in Idaho. McCowan and Rudinsky (1958) reported an average of about 10 eggs for each inch of gallery in logs examined during an outbreak near Coos Bay, Oregon. The average length of gallery for successful beetles was 8.5 inches. Walters and McMullen (1956), working in British Columbia, listed average galleries ranging from 8 to 10 inches. Evenden and Wright (1955) reported an average gallery length of 5 to 12 inches in western North America. The average length of successful galleries for our three study sections was 8.5 inches.

Figure 5 illustrates the average number of eggs laid in each inch of egg gallery for 51 galleries, classified by gallery length. The first and last inch of gallery usually contained the fewest eggs, which partially explains why the average number of eggs to an inch was less in short galleries (less than 5 inches) than in long galleries (greater than 5 inches). After reaching a peak in the second or third inch of gallery, the number of eggs laid decreased in succeeding inches in all but 2 of the 12 classes. Bedard (1933) observed similar distribution after examining 376 galleries constructed in host trees from stands of interior type.

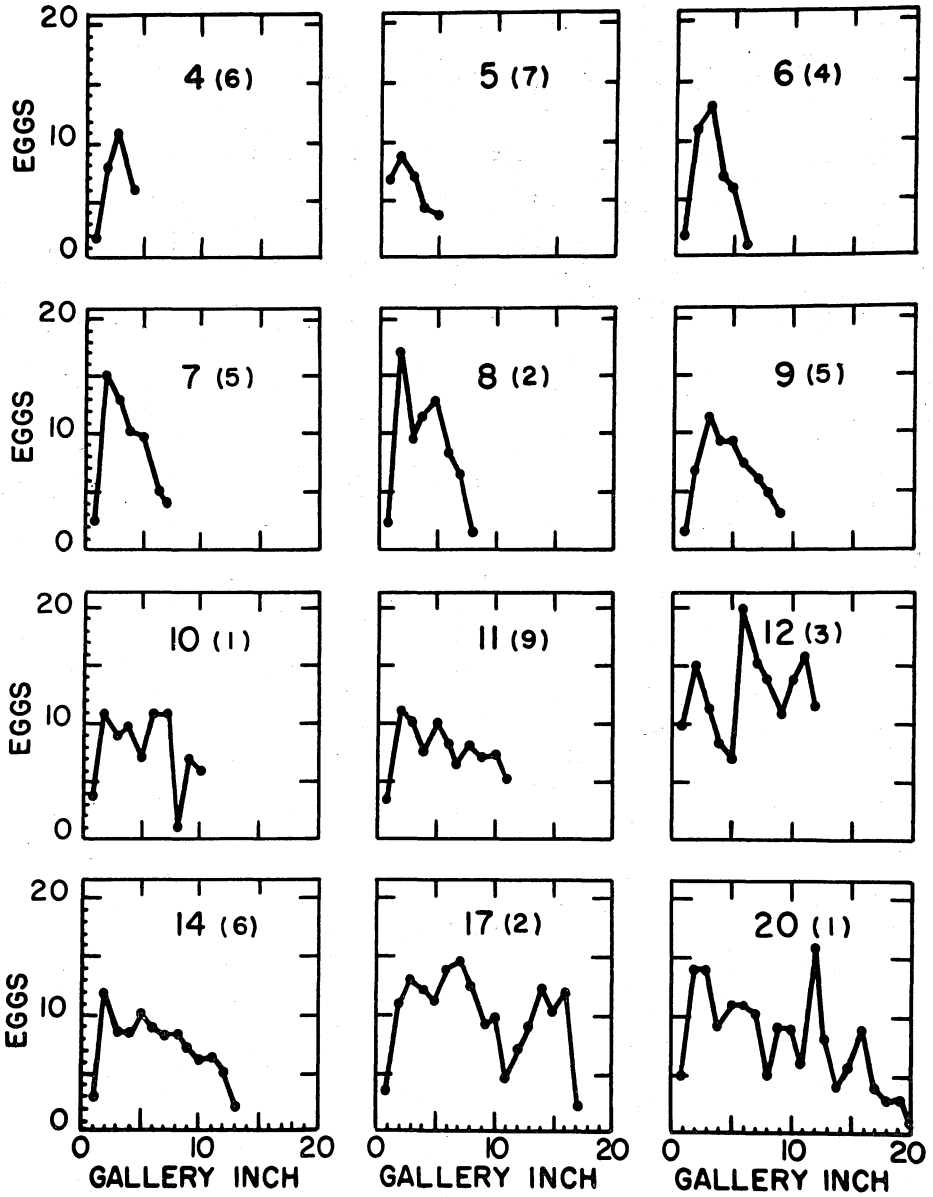


Figure 5. Average number of eggs laid in each inch of egg gallery for 12 selected gallery lengths shown in inches with number of galleries of each length in parentheses.

Table 2. Abundance of Insect-eating Insects on the Bottom, Middle, and Top Sampling Positions of 14 Study Trees Examined during 1960 at Areas A and B and Averages at Each Area in Insects Per Square Foot.

Parasites and predators								
Coeloides brunneri			Clerid larvae			Diptera larvae		
Bot	Mid	Top	Bot	Mid	Top	Bot	Mid	Top
East Trail (area A)								
0	0	0	0.0	0.3	--	0	3.6	--
0	0	0	0.0	0.0	0.1	0	0.0	0.1
0	0	0	0.0	0.3	--	0	1.6	--
0	0	0	0.1	0.0	--	0	4.0	0.0
0	0	0	0.0	0.1	0.0	0	0.0	0.0
0	0	0	0.0	0.0	--	0	0.0	0.0
0[1]	0	0	0.01	0.1	0.01	0	1.5	0.01
Woods Creek (area B)								
0.1	3.5	6.6	0.1	0.7	1.0	5.0	12.3	2.3
0.0	0.0	2.6	1.7	0.4	1.2	2.8	3.9	3.2
0.5	0.6	1.2	1.1	0.5	0.4	3.5	6.7	1.7
1.6	5.1	1.9	0.6	0.9	1.1	3.1	5.7	5.1
0.0	3.9	4.4	0.5	0.2	0.2	1.2	6.1	4.5
0.2	0.1	0.7	1.6	0.4	0.7	2.0	3.5	2.2
0.6	7.0	2.8	1.1	0.4	1.0	5.3	2.1	2.7
0.2	1.2	4.1	0.9	0.9	0.7	4.6	7.4	5.1
0.5[1]	2.7	3.1	1.0	0.5	0.8	3.5	6.1	3.3

[1] Average for each area.

Table 3. The Number of Beetles Introduced into a Caged Bole Section Compared to the Final Density of Attack.

Bole	Bark surface	Beetles introduced		Attacks	
		Females	Males	Total	Density
	Sq ft			Per bole	Per sq ft
A-1	9.0	12	15	11	1.2
A-2	9.6	32	35	25	2.6
A-3	9.6	63	65	31	3.2
B-1	9.0	14	17	5	0.6
B-2	9.6	45	50	16	1.7
B-3	9.9	61	65	36	3.6

Figure 6. Douglas-fir beetle gallery showing the area of unmined phloem between successive groups of larval mines as indicated by the arrows.

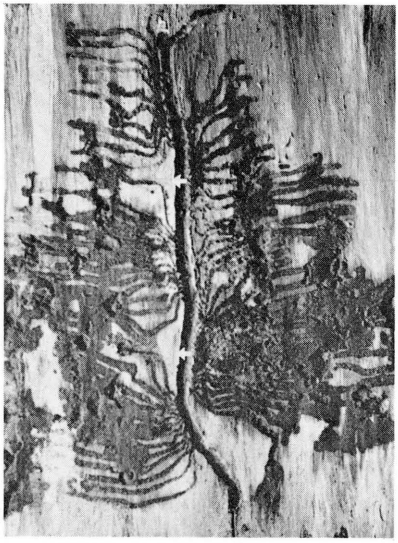
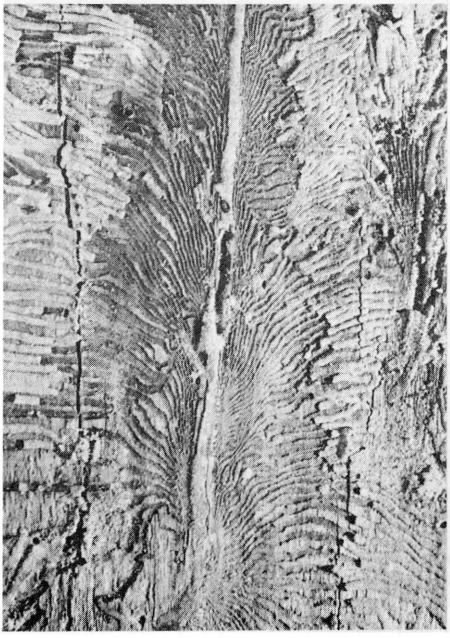


Figure 7. Portions of two Douglas-fir beetle galleries showing how the phloem between successive groups of larval mines is more completely mined as the number of larval mines increase from medium (left) to high densities (right).



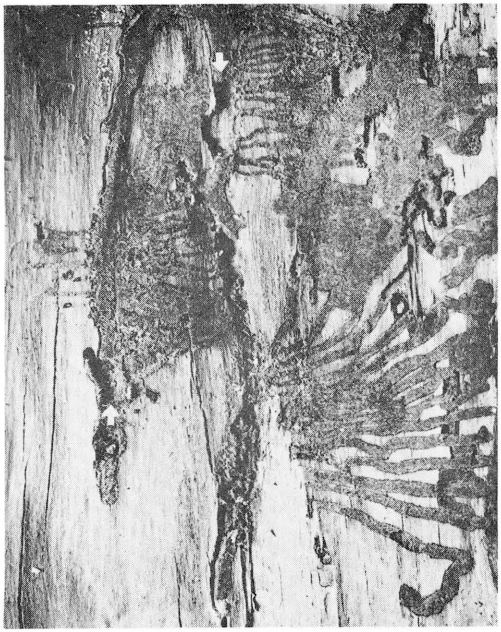


Figure 8. A $\frac{1}{4}$-square-foot developmental area (6 by 6 inches) showing utilization of the phloem by a single Douglas-fir beetle brood. Arrows show the direction of gallery construction. In the space between the right-hand edge of the area and the right-hand portion of the egg gallery, 14 percent of the brood survived to the callow adult stage.

Figure 9. A $\frac{1}{2}$-square-foot developmental area (6 by 12 inches) showing utilization of the phloem by a single Douglas-fir beetle brood. A total of 65 larval mines were present on the right side of the egg gallery with 55 percent surviving to the callow adult stage. No brood reached the callow adult stage on the left side.

Figure 10. A 1-square-foot developmental area showing the utilization of the phloem by a single Douglas-fir beetle brood. Final survival reached 30 percent.

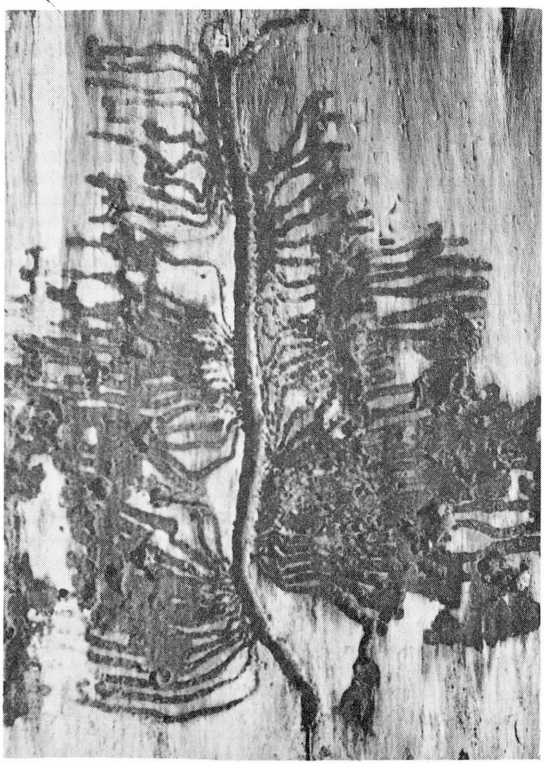


Figure 11. A $1\frac{1}{2}$-square-foot developmental area showing utilization of the phloem by a single Douglas-fir beetle brood. Seventy-six percent of the brood reached the callow adult stage.

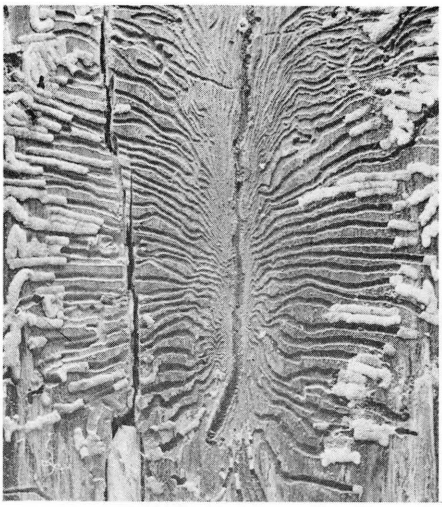


Figure 12. Low intensity of intra-specific competition. The area shown had a larval mine density of 64 to the square foot and brood survival reached 32 percent.

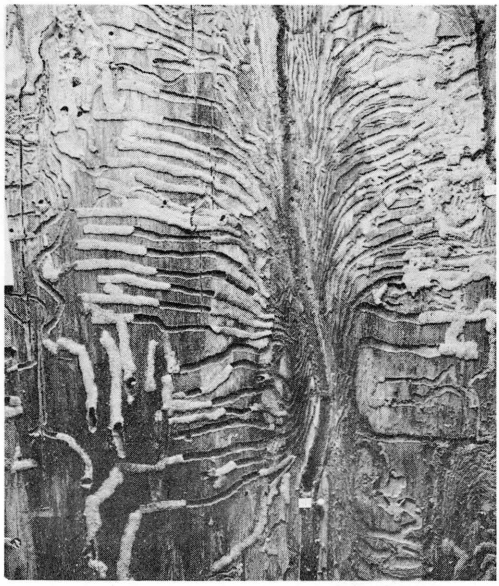


Figure 13. Low intensity of intra-specific competition. The area between the two egg galleries had a density of 74 larval mines to the square foot and a final survival of 30 percent. The area to the left of the central egg gallery had a density of 60 larval mines to the square foot and final survival of 64 percent.

We also tabulated data (Table 5) to compare the number of eggs deposited on the left and right side of egg galleries established in three bole sections. The division of eggs between sides of the gallery was about equal. This type of alternate arrangement furnishes a greater chance for larval survival than would be possible if the eggs were all laid on the same side of the gallery. The distance between successive egg groups on the same side of the egg gallery was measured on 50 galleries to determine the variation and possible effect on brood survival. Separation of the 50 galleries into two groups, one comprising galleries 10 inches and less in length, and a second group consisting of galleries longer than 10 inches, revealed this distance to average 0.3 of an inch more in the longer galleries. This difference in the average distance between egg groups did not have measurable effect on brood survival.

The re-emergence of adult beetles from six bole sections used to measure the number of eggs laid is shown in Table 6. This re-

emergence took place during 34 days following the last day beetles were introduced into the cages; 74 percent of the parent beetles re-emerged during the first 17 days of this period.

McMullen and Atkins (1961) reported that more parent Douglas-fir beetles emerged from egg galleries at attack densities greater than 5 to a square foot than at densities below this level. In our study, proportionately more females emerged from the bole sections infested to a density of 3 attacks to the square foot. Few instances were noted where extension of one gallery by a female beetle was restricted by the presence of another gallery. The reason for the re-emergence of the female beetles is unknown; Reid (1962), however, has observed that female mountain pine beetles (Dendroctonus ponderosae Hopkins = monticolae) change from the egg laying to the flight condition and leave the egg gallery when the phloem tissue begins to dry.

Oviposition and gallery pattern

Trägardh (1930) noted in his early studies of gallery patterns of bark beetles native to Europe that brood survival depended in part on the arrangement of the larval mines. He felt the necessity for minimizing the danger of starvation from a dense population and the need for economically utilizing the available food were the two factors to which bark beetle galleries owed their origin.

The gallery pattern created by the larvae of Douglas-fir beetle broods can be traced to the arrangement of the eggs. Initially, the pattern resulting from the larval mines is governed by the alternate distribution from side to side of the egg pockets along the gallery. Once the larvae have mined several inches from the egg gallery, however, their direction seems to be regulated in part by deterioration of the surrounding phloem tissue which is frequently associated with the presence of blue staining fungi. Larvae also avoid areas of phloem that are covered with white fungal mats. The mining larvae perhaps are guided by sounds from the movement and feeding of adjacent larvae.

While the survival of a Douglas-fir beetle larva depends to a considerable extent on the density of eggs for each unit area, the amount of phloem available to the early larval stages is related to the arrangement of eggs in the egg gallery. Examination of the gallery pattern of the Douglas-fir beetle shows that the width of larval mines increases as the larvae mine away from the egg gallery. This enlarged width results from the greater size and increased food requirements of the larvae as they grow (Figure 6). Figure 6 also reveals that the pattern of egg deposition provides an area of phloem that is not used initially between successive egg groups on the same side of the egg gallery. As

Table 4. Average Number of Eggs Laid in Three Study Sections, Classified by Gallery Length.

Length of parent gallery[1]	Number of galleries	Total length[2]	Total eggs	Eggs per gallery	Eggs per inch of gallery[3]
Inches		Inches			
0.0- 1	0	--	--	--	--
1.1- 2	3	4.7	11	3.7	2.3
2.1- 3	1	2.5	5	5.0	2.0
3.1- 4	6	24.0	166	27.6	6.9
4.1- 5	7	34.1	235	33.6	6.9
5.1- 6	4	23.3	172	43.0	7.4
6.1- 7	5	34.1	295	60.0	7.0
7.1- 8	2	16.0	140	70.0	8.7
8.1- 9	5	45.0	303	60.6	6.7
9.1-10	1	9.9	77	77.0	7.8
10.1-11	9	96.3	761	84.5	7.9
11.1-12	3	35.6	309	103.0	8.7
12.1-13	1	13.0	119	119.0	9.1
13.1-14	6	82.0	635	105.8	7.7
14.1-15	0	--	--	--	--
15.1-16	0	--	--	--	--
16.1-17	2	33.0	306	153.0	9.3
17.1-18	0	--	--	--	--
18.1-19	0	--	--	--	--
19.1-20	1	20.0	157	157.0	7.8

[1] There also were 11 unsuccessful attempts at galleries.

[2] Successful galleries averaged 8.5 inches.

[3] Average number of eggs in each inch of gallery was 7.7; least significant difference was 1.5.

Table 5. Comparison of the Number of Eggs Laid on the Left and Right Side of Egg Galleries in Three Bole Sections in the Laboratory in 1961.

Bole	Galleries examined	Total eggs laid	
		Left	Right
B-1	4	40	65
A-2	21	806	1,010
A-3	31	841	841

Table 6. Re-emergence of Parent Adult Beetles from Six Bole Sections in the Laboratory in 1961.

Bole	Total attacks	Re-emergence			
		Females	Males	Females	Males
		Number		Percent	
A-1	11	1	4	9	36
A-2	25	2	8	8	32
A-3	31	9	17	29	55
B-1	5	0	1	0	20
B-2	16	8	8	12	50
B-3	36	17	17	55	47

the width of the mines increase and additional phloem tissue is required for development, the larvae are forced to turn into this region. Figure 7 illustrates how the larvae in a gallery with a high number of eggs for each inch of gallery almost entirely utilize the phloem between successive egg groups. An even more complete utilization of this region of phloem tissue was a result of competition for phloem between larvae from adjacent galleries (Figure 7).

Egg gallery density and oviposition pattern

Eggs averaged 6.5, 8.1, and 8.7 for each inch of parent gallery at densities of attack of 1.2, 2.8, and 3.2 for each square foot in bole sections studied. Failure to establish higher densities of attack precluded determination of the effect of overcrowding on egg deposition.

Female beetles at low densities of attack made galleries shorter than those of beetles in boles infested to high densities. Successful egg galleries averaged 4.5, 10.2, and 8.7 inches long at attack densities of 1.2, 2.8, and 3.2 for each square foot.

Denton (1950) reported that egg galleries of the beetle, Ips perturbatus (Eichoff), constructed in close proximity and parallel to one another often contained eggs only on the side of the gallery away from the adjoining gallery. Examination of pattern of attack on the three bole sections revealed that this arrangement did not occur with Dendroctonus pseudotsugae. The data were recorded in the laboratory from three pairs of galleries constructed with the members of each parallel to one another and less than $\frac{1}{2}$ inch apart. These paired galleries (Table 7) were examined before the eggs hatched, so the galleries of each pair were probably constructed simultaneously. Mining by a female beetle and the resultant change in the phloem tissue along the edges of the egg gallery apparently did not affect the oviposition habit of the adjacent female.

Table 7. Comparison of the Number of Eggs Laid in the Laboratory on the Left and Right Side of Three Pairs of Egg Galleries Less Than 1/2 Inch Apart.

Gallery pair	Eggs per gallery		Eggs per inch of egg gallery
	Left	Right	
14	64	57	8.2
11	35	63	8.6
2	73	59	9.4
4	31	88	9.1
3	51	55	9.6
4	31	88	9.1

Inability to obtain the desired densities of invasion precluded determination of the effect of density of invasion on the number of eggs laid. The oviposition studies do reveal, however, that although the number of eggs laid reaches a peak in the first few inches of gallery, the distance between successive egg groups and the alternate arrangement of egg groups serve as mechanisms that minimize the possibility of starvation.

Phloem Tissue Utilized During Brood Development

Of the 120 developmental areas of infested bark, only 27 contained live brood. Of these, four had their gallery pattern destroyed by the mining of callow (incompletely developed) adults. The low success may have been caused by the low density of attack and the resinous condition of some bole sections used for the study. Table 8 lists the percentage of the total number of successfully infested areas of each size that contained callow adults.

Survival of broods varied considerably within and between developmental areas (Table 9). This range in survival was largely attributable to the difference in number of eggs laid between developmental areas. If the average gallery length of 10 to 12 inches, with 8 eggs to the inch had been constructed, the larval development in the $\frac{1}{2}$- and 1-square-foot areas might have been severely restricted. In many instances, however, so few eggs were laid that the areas contained more phloem than was needed for development and survival of the larvae

Table 8. Number and Percentage of the Developmental Areas of Each Size Containing Callow Adult Douglas-fir Beetles.

Area size	Areas infested	Areas with callow adults	
		Number	Percentage
Sq ft			Percent
1/4	8	1	12
1/2	20	8	40
1	20	7	35
1 1/2	8	3	37
2	8	2	25
3	8	2	25

Table 9. Percentage of Douglas-fir Beetle Brood Surviving in Various Areas of Phloem Available in the Laboratory.

Area of phloem tissue, sq ft					
1/4	1/2	1	1 1/2	2	3
14	8	19	62	50	19
	15	30	76	56	72
	30	34	80		
	40	64			
	45	76			
	55	76			
	65	88			
	88	—	—	—	—
Avg	43	55	76	53	45

present. For this reason, we counted the developing larvae and measured the area of phloem tissue they utilized in each section. The survival percentages were grouped into three classes based on the phloem factor. The first class contained broods that had mined an area of phloem tissue equivalent to providing each larva with from 0 to 1 square inch of phloem. The second and third classes ranged from 1.1 to 1.5 and from 1.6 to 1.9 square inches. The results were as follows:

Phloem factor class	Number of broods	Average brood survival
		Percent
0.1 - 1.0	7	31
1.1 - 1.5	10	60
1.6 - 2.0	6	64

Thus, there was a marked increase in brood survival when each larva had 1 square inch or more of phloem in which to develop.

Restricted larval development in many areas and mining by callow adults destroyed much of the gallery pattern and rendered difficult the measurement of individual larval mines. The length of three larval mines from each developmental area was measured, however. The lengths ranged from 4.5 to 6.0 inches, with an average of 5.3 inches. In general, the longer mines seemed to be located in areas where larval competition was intense.

Figures 8 through 11 show patterns of larval mines in developmental areas of $\frac{1}{4}$, $\frac{1}{2}$, 1 and $1\frac{1}{2}$ square feet. Figure 8 illustrates how the dimensions of the $\frac{1}{4}$-square-foot developmental area limited the normal upward extension of this egg gallery. As a result, the beetle reversed its normal upward extension, and in turning downward, confined larvae in the area between the two portions of the gallery. The distance between the right-hand portion of the egg gallery and the right-hand edge of the area was 3 inches, yet larvae were forced to double back to complete their development. The phloem factor for the area to the right of the egg gallery was 0.65 square inch for each larva, and 14 percent of the larvae survived. In Figure 9, the width of the phloem tissue between the egg gallery and the right-hand edge of the area was 3.8 inches, and the corresponding width on the left side was 2.2 inches. The phloem factor and survival for the right side were 0.60 and 55 percent. The phloem factor on the left side was 0.38 and no larvae survived. Figure 10 illustrates the gallery pattern in a 1-square-foot area. The phloem factor was 1.2 and survival reached 30 percent. The length of larval mines averaged 5.1 inches. Figure 11 shows the larval mine pattern in a $1\frac{1}{2}$-square-foot developmental area. The phloem factor equaled 1.2 square inches of phloem per larva, and survival reached 76 percent. Larval mines averaged 5.7 inches in length.

Our observations and results are similar to those obtained by Johnson (1962) during a study designed to determine the optimum size of rearing slab for the Douglas-fir beetle. He was able to show that beetle survival increased significantly when the slab was increased in width from 4 to 8 inches and the length was increased from 8 to 24 inches.

Field Studies of Intraspecific Competition

As happened in earlier studies, brood did not develop successfully in several of the caged study sections. After the female beetles had constructed several inches of egg gallery in the down study tree at area D, the phloem evidently became unsuitable to the ovipositing beetles, and they left the tree. Interestingly, the wild population of

Douglas-fir beetles was attacking this tree during May when the cages were being placed on the tree, which seems to indicate that the tree was suitable to the beetles early in the season. When the beetles left the tree, the phloem tissue was still moist and showed no sign of deterioration. In contrast, the down study tree at area C remained suitable in all sections, although we had some difficulty in attaining the desired densities of invasion on the caged and uncaged areas of this tree.

Although the bole sections were successfully infested, development of the brood was largely unsuccessful, so little or no intraspecific competition resulted. The pattern of galleries on the inner bark indicated that the bole sections became unsuitable for the larvae in the early instars, and the brood died before completing development.

Final attack densities on the study sections

The final densities of attack and survival of broods in the caged and uncaged areas on the down study tree at area C are shown in Table 10. Only the low density of 1 attack to the square foot was attained consistently; the desired densities of 3 for each square foot (medium) and 8 or more for each square foot (high) were infrequent on the caged study sections. New attacks were seldom recorded after attack densities reached 2 to 3 to the square foot. In addition, attacks were not evenly distributed over the caged sections. Although the caged sections as a whole did not receive the intended range in attacks, smaller portions of each section showed the desired range in attack density. Attacks by the wild population were more abundant than anticipated, and, with the exception of sections 5, 6 and 11, 12, the dense attack prevented establishment of comparable densities in caged and uncaged sections.

Densities of predators and parasites recorded under the bark during sampling were surprisingly low in view of the apparent abundance of certain species in the study area (Table 11). Minutes after the experimental tree was felled at study area C during June, Douglas-fir beetles and clerids, Enoclerus sphegeus Fabricius and E. lecontei Wolcott, appeared on the bark. The predaceous fly, Medetera sp., and the parasite, Coeloides brunneri Viereck, were much less abundant at that time. The low density of clerid larvae beneath the bark may have resulted because the larvae bored into the outer bark or migrated to the duff in midsummer (Kline and Rudinsky, 1964; Cowan and Nagel, 1965). Although both habitats were examined, no larvae were found. The scarcity of predaceous and parasitic insects in the logs may have been caused by the low level of population of the Douglas-fir beetle in the Marys Peak area.

The number of pairs of beetles theoretically needed to infest the

Table 10. Douglas-fir Beetle Attacks to a Square Foot of Bark and Percent Survival of the Broods in the Six Caged and Six Uncaged Areas on the Down Study Tree at Area C in 1961.

Section	Desired density	Bark area	Final attack density		Survival
			Successful[1]	Unsuccessful[2]	
		Square feet	Per square foot		Percent
1 (Caged)	Low	18.0	0.5	0.3	37
2	Low	18.1	4.5	1.2	1
3 (Caged)	Medium	18.4	0.8	0.2	17
4	Medium	16.7	3.5	0.7	4
5 (Caged)	High	16.0	3.1	1.2	20
6	High	15.8	2.5	0.7	20
7 (Caged)	Low	15.4	0.5	0.1	46
8	Low	15.0	2.4	0.6	24
9 (Caged)	Medium	14.8	1.6	0.5	19
10	Medium	14.4	4.4	0.6	6
11 (Caged)	High	13.7	3.8	2.9	15
12	High	14.7	3.8	0.7	4

[1] Attacks having at least one larval mine originating from the egg gallery.

[2] Attacks without a larval mine originating from the egg gallery.

Table 11. Average Number of Predaceous and Parasitic Insects Found under the Bark of the Uncaged Study Sections on the Experimental Tree at Area C in 1961.

Section	Number of predators and parasites		
	Diptera	Cleridae	Coeloides sp.
2	3	2	0
4	6	1	0
6	2	2	0
8	0	2	0
10	3	1	0
12	2	0	0

caged sections was calculated by multiplying the desired attack density by the square-foot area in each section. Medium and high densities desired were not attained on some sections even when the number of beetles introduced into the cages exceeded the calculated number (Table 12). The maximum period during which beetles continued their attacks was 11 days. After this time, beetles continued to crawl about the cages until they died. Unsuccessful attacks averaged 0.87 and 0.75 to a square foot on the caged and uncaged sections. At the high density of attack, the number of unsuccessful attacks in the caged sections increased noticeably, but remained close to the average in the uncaged sections.

Attack density and brood survival

The relation that we found between density of attacks and the number of surviving progeny (Table 13) differed from that obtained by McMullen and Atkins (1961), but they sampled during the spring, following the year of attack, rather than during the fall, following initial attack. They reported the maximum number of progeny were produced when the attacks numbered about 4 to 8 to a square foot, and total length of galleries ranged from 30 to 60 inches for each square foot. They also found the increase in progeny dropped to a ratio of 1:1 at densities of 13 to 17 attacks for each square foot. In our study, we noted an increase ratio of about 1:1 at densities of 3 to 6 attacks to the square foot. While the reasons for these differences are not known, differences in host trees and beetle populations could possibly account for some of the variation.

In our investigation, the maximum number of progeny resulted when the attacks were no more frequent than 2 to a square foot. Attacks fewer than 1 to a square foot resulted in fewer surviving progeny for each square foot than were recorded at densities of 1.0 to 1.9 attacks to a square foot. Reduction in survival at less than 1 attack to a square foot corroborates results obtained from laboratory studies where 85 percent of the attacks were unsuccessful at 1 attack for each 1.5 square feet of bark. While the cause for this lower survival and success of attack at low densities of attack was not determined, the phloem tissue seems unsuitable for gallery construction until attacks reach from 1 to 2 for each square foot. Perhaps green phloem of down trees still presents some form of resistance to invading beetles that must be overcome somewhat as a live standing tree is overcome by a mass attack of beetles, or perhaps initial attacks in sufficient density reduce the moisture content to a more favorable level.

Data in Table 13 emphasize the importance of attack density in brood survival. At densities averaging less than 1 attack for each square foot, there is sufficient inner bark available for unrestricted

development, but survival of individual broods is affected by the resistance of the tissue to boring of the beetles, by excessive moisture in the phloem, or by some unknown factor. When densities above 2 to 3 attacks for each square foot are reached, and resistance of the tissue to

Table 12. Square-foot Areas of Bark, Number of Douglas-fir Beetles Introduced to a Cage, and Final Attack Densities for the Six Caged Sections on the Down Tree at Area C in 1961.

Cage	Bark area	Beetles introduced	Attack density	
			Successful[1]	Unsuccessful[2]
	Sq ft	Pairs	Per square foot	
1	18.0	8	0.5	0.3
3	18.4	20	0.8	0.2
5	16.0	145	3.1	1.2
7	15.4	7	0.5	0.1
9	14.8	30	1.6	0.5
11	13.7	195	3.8	2.9

[1] At least one larval mine originating from the egg gallery.

[2] Attacks without a larval mine originating from the egg gallery.

Table 13. Effect of Attack Density on the Average Length of Egg Gallery, Number of Larval Mines, Number of Progeny, and Survival of the Douglas-fir Beetle in the Study Tree at Area C in 1961.

Attacks	Gallery length	Larval mines	Progeny	Survival
Per sq ft	Inches	Per sq ft	Per sq ft	Percent
0.0 - 0.9	11.8	50	21	36
1.0 - 1.9	10.9	77	37	45
2.0 - 2.9	10.5	83	24	32
3.0 - 3.9	7.7	140	10	10
4.0 - 4.9	8.5	169	12	7
5.0 - 5.9	7.8	186	13	7
6.0 - 6.9	8.0	177	10	5
7.0 - 7.9	7.6	238	13	6
8.0 - 8.9	7.7	242	9	3
9.0 - 9.9	7.2	204	3	1
10.0 - 10.9	8.7	252	6	2
13.0 - 13.9	5.7	235	2	1

Table 14. Effect of Total Length of Egg Gallery to the Square Foot on the Average Gallery Length, Larval Mines, Progeny, and Survival of the Douglas-fir Beetle in Study Tree at Area C in 1961.

Length of successful gallery		Larval mines	Progeny	Survival
Total	Average			
		Per	Per	
Inches	Inches	sq ft	sq ft	Percent
2-19	16.4	62	24	38
20-39	9.2	125	19	20
40-59	9.8	193	13	7
60-79	8.1	237	7	3
80-100	9.0	242	7	3

Table 15. Effect of Larval Mine Density on the Average Gallery Length, Number of Progeny, and Survival of the Douglas-fir Beetle in the Study Tree at Area C in 1961.

Larval mines	Gallery length	Progeny	Survival
Per		Per	
sq ft	Inches	sq ft	Percent
18- 50	8.3	9	29
51-100	11.9	30	42
101-150	8.8	19	17
151-200	8.6	11	6
201-250	8.1	8	3
251-300	8.2	7	2
301-325	10.0	8	2

Table 16. A Comparison of the Number of Successful Attacks and Larval Mines to a Square Foot of Bark with the Number of Surviving Progeny.

Successful attacks	Larval mines	Increase ratio
0.5-0.9	50	1:14.0
1.0-1.9	77	1:12.0
2.0-2.9	83	1:6.0
3.0-3.9	140	1:1.4
5.0-5.9	186	1:1.2
6.0-6.9	177	1:1.3
7.0-7.9	238	1:2.0
8.0-8.9	242	1:0.1
13.0-13.9	235	1:0.0

boring is no longer an important factor, intraspecific competition takes place and reduces survival.

We did not correlate density of attack and length of egg gallery, because attack densities greater than 5 to a square foot did not reduce the length of galleries constructed by invading females. At these densities, egg galleries alone do not occupy enough phloem to interfere with gallery construction. There was some indication, however, that presence of mature larvae from early attacks did shorten the galleries of later attacks.

The number of larval mines to a square foot increased with increasing density of attack. At the greater larval densities, the number of survivors (callow adults) decreased. We show the relation between length of egg gallery for a square foot and number of larval mines and brood survival in Table 14. Although the number of larval mines increased at the higher densities of egg gallery, the average length of the galleries showed little change.

Survival decreased progressively above and below the optimum of 50 to 100 larval mines to a square foot (Table 15). Survival was notably less at densities above 201 to 250 larval mines to a square foot. Figures 12 through 16 illustrate Douglas-fir beetle galleries with larval mines ranging in density from 64 to 231 to a square foot on the study tree at area C.

To compare brood survival with the area of inner bark available to each larva, the phloem factors for 100 samples from the tree at area C were divided into seven classes:

Phloem factor class	Brood survival
Sq inches	Percent
0.4 - 1.0	5
1.1 - 1.5	22
1.6 - 2.0	35
2.1 - 2.5	47
2.6 - 3.0	52
3.1 - 3.5	24
3.6 - 8.0	36

The results differed slightly from the laboratory studies in which 64 percent of the brood survived when the phloem factor ranged from 1.6 to 2.0. In the tabulation, maximum survival of brood resulted when the phloem factor ranged from 2.6 to 3.0. When the area of phloem per larva exceeded this range, survival declined. As we already discussed,

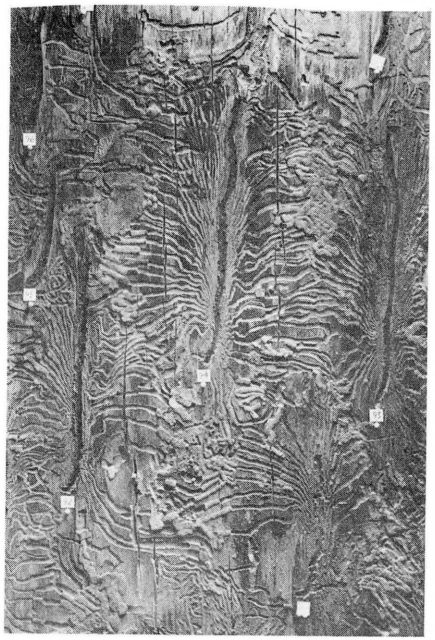


Figure 14. Moderate intensity of intraspecific competition. The area shown had a larval mine density of 109 to the square foot and a final survival of 20 percent.

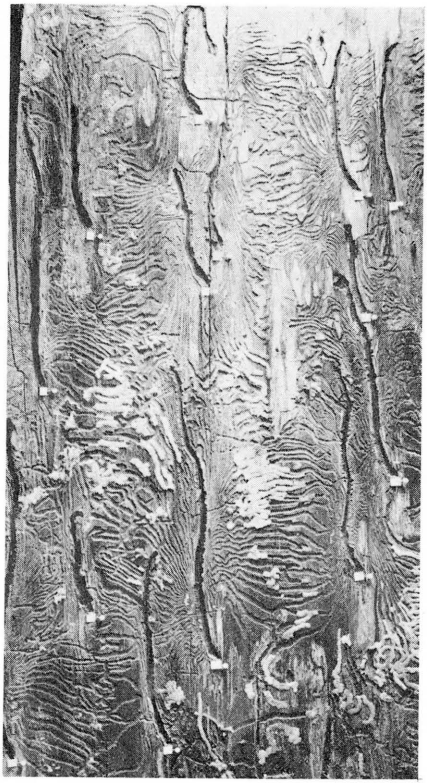


Figure 15. Intense intraspecific competition. The area shown had a larval mine density of 205 to the square foot and a final survival of 4 percent.

Figure 16. Intense intraspecific competition. The area within the boundaries of the string had a larval mine density of 231 to the square foot and a final survival of 0.6 percent.

this decline in survival reflects the unfavorable interaction of host material with the sparse attacks of beetles.

The difference at which maximum survival of brood occurred in the field and laboratory may indicate that phloem from different trees or of different age varies in its ability to meet the feeding requirements of larvae. Variations in the beetles themselves may also be responsible for the differences. The beetles studied in the laboratory and the field experiments were, however, obtained from the same tree.

We also compared density of attack and survival by computing the "increase ratio" or the ratio between the number of pairs of attacking parents and number of progeny. Again, brood survival decreased with increasing density of attack (Table 16). The highest increase ratio occurred at less than 1 attack and 50 larval mines to a square foot. The ratio of increase was fairly constant between 3 and 8 attacks for each square foot; thereafter, it declined markedly.

Area of phloem mined by individual larvae

The area of phloem mined by each of 60 larvae ranged from 0.8

Table 17. Average[1] Thickness of Phloem, Maximum Depth of Larval Feeding, Length of Larval Mine, and Total Area of Phloem Mined by 60 Larvae from the Study Tree at Area C in 1961.

Section	Depth of phloem	Depth of feeding	Length of mines	Area mined
	Mm	Mm	Cm	Sq in.
1	4.4	1.2	15.4	1.1
2	4.4	1.0	15.4	0.9
3	4.6	0.9	14.8	1.0
4	4.3	1.0	14.1	1.0
5	4.3	1.0	15.9	0.9
6	4.2	1.0	16.5	1.0
7	3.4	1.1	15.3	1.0
8	4.3	1.1	16.0	1.0
9	4.4	1.0	16.4	1.0
10	4.8	1.0	16.1	1.0
11	4.4	1.4	15.1	1.1
12	4.3	1.1	15.0	1.0
All	4.9	1.1	15.7 (6.2 inches)	1.0

[1] Based on five galleries to a section.

to 1.4 square inches and averaged 1.0 square inch (Table 17). The phloem ranged from 3.7 to 5.2 millimeters in thickness. In cross section, mines of the larvae ranged from 0.7 to 1.6 millimeters and averaged 1.1 millimeters at their deepest points.

The larval mines in the phloem are hemispherical in cross section. The depth of feeding increased little between the four stages of larval development. This lack of change probably resulted because the larvae had not been forced to compete for space and ample phloem was available to them. The almost total mining of this tissue in crowded areas prevented accurate measurement of the depth of larval feeding, the length of larval mines, and the final areas of inner bark mined.

Field Studies of Interspecific Competition

Little interspecific competition was observed during the study. Absence of interspecific competition was attributed to three circumstances: the low population levels of associated phloem-feeding insects in relation to the abundance of host material; the time of flight and attack of the associated species; and the part of the tree that was infested by the various phloem-feeding species. For example, flight of the scolytid, Pseudohylesinus nebulosus (LeConte), precedes the flight of the Douglas-fir beetle (Daterman, Rudinsky, and Nagel 1965) and also, at low population levels, occupies the top portion of the trunk and branches, which are usually avoided by the Douglas-fir beetle. Attacks by the Douglas-fir beetle were followed by other beetles, Scolytus unispinosus LeConte and Dryocetes autographus (Ratzeburg). In the study trees, S. unispinosus infested the topmost portion of the bole, an area not usually infested by the Douglas-fir beetle, but Pseudohylesinus nebulosus infested only branches, although it is known to infest the tops of tree trunks (Walters and McMullen, 1956). Dryocetes autographus infested areas occupied by the Douglas-fir beetle, but the density was too low to measure effect of interspecific competition on survival.

In trees exposed to the sun, the buprestid, Melanophila drummondi (Kirby), occupied the skyward portion of the bole; this portion is usually avoided by the Douglas-fir beetle. Little interspecific competition resulted even along borders of shaded and sun-exposed areas because the phloem in this region was too dry for Douglas-fir beetles to survive, and the larvae died before competition occurred. These observations indicate that interspecific competition is an important natural control factor when populations of the Douglas-fir beetle and associated scolytids greatly exceed that encountered in this study, when perhaps they are forced into areas of the tree that they do not occupy at low density.

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